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# Oviposition behavior of *Trichogramma Platneri* (Hymenoptera) on clustered hosts

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**OVIPOSITION BEHAVIOR OF *TRICHOGRAMMA PLATNERI* (HYMENOPTERA)  
ON CLUSTERED HOSTS**

**A Thesis**

**Presented to**

**The Faculty of the Department of Biological Sciences**

**San Jose State University**

**In Partial Fulfillment**

**of the Requirement for the Degree**

**Master of Science**

**by**

**Zia Nisani**

**May 2002**

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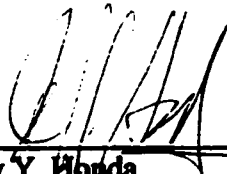
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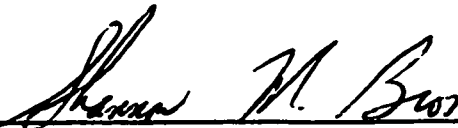
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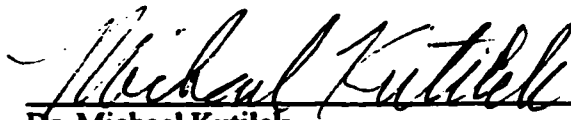
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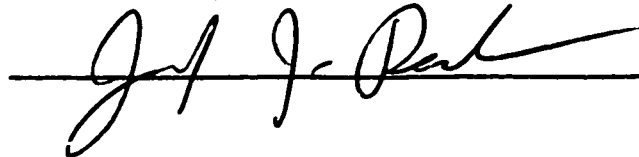


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## **ABSTRACT**

### **OVIPOSITION BEHAVIOR OF *TRICHOGRAMMA PLATNERI* (HYMENOPTERA) ON CLUSTERED HOSTS**

by Zia Nisani

The oviposition behavior of *Trichogramma platneri* on clustered hosts was measured at 3 and 24-h periods. This study did not show any significant relationship between host size and the number of progeny allocated per host regardless of either time period studied. The data suggest that *Trichogramma* adjust their clutch size over time. In 3-h parasitization about 76% of hosts were allocated 2 progeny while in 24-h parasitization only 42% were allocated the same complement. *Trichogramma platneri* seem to respond to clustered hosts by using ovipositional experience in adjusting clutch size.



## **ACKNOWLEDGMENTS**

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## INTRODUCTION

The ability of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) to measure host volume is important because resources available in each host egg are limited both spatially and temporally. Larval competition for nutrients within the host will result if too many progeny are allocated to a single host (Klomp & Teerink, 1967), at the same time allocating too few progeny to each host puts the wasp at risk of not depositing its egg complement (Klomp & Teerink, 1967; Waage & Ng, 1984). Furthermore, ovipositing few eggs within the host increases the risk of bacterial growth due to excess moisture that could be detrimental to developing larvae (Hoffman *et al.*, 1975).

Female *Trichogramma* examine potential host eggs by walking back and forth over them while continuously drumming the surface with their antennae (Salt, 1935; Klomp & Teerink, 1962; Schmidt & Smith, 1989). The initial examination transit that *Trichogramma* employ is usually a straight line that brings the parasitoid to the highest point of the host egg relative to the substrate (Schmidt & Smith, 1989). This initial examination continues until the wasp makes contact with the substrate on the opposite side of the egg from its starting point. When the antennae make contact with the substrate the wasp briefly pauses and then turns and continues the examination in another direction (Schmidt & Smith, 1989). This external measurement of the host surface area is important in determining the number of progeny that are allocated to it, and *Trichogramma* adjust their clutch size in response to these measurements (Schmidt & Smith, 1987a, 1987b, 1985b).

By artificially reducing the initial *Trichogramma* transit across the host egg, Schmidt & Smith (1985a, 1987b) demonstrated that clutch size decreased and concluded that initial transit and surface area measurement is used by these wasps in adjusting the number of progeny allocated. Additionally, hosts having similar volumes but differing in their exposed surface area are allocated fewer progeny. *Trichogramma* allocated approximately 1.8X more progeny to fully exposed hosts than partially exposed hosts (Schmidt & Smith 1985b). They summarized that as the surface area increases, the number of edge turns performed by the wasp during its transit walk decreases; resulting in the allocation of a larger clutch size within the host.

*Trichogramma* also appear to respond to different hosts densities. As host density increases, females reduce the number of progeny allocated to each host which in turn increases offspring fitness (Klomp & Teerink, 1967; Hirose *et al.*, 1976; Charnov & Skinner, 1985). If female wasps were able to count the number of hosts available in an egg-mass, then it would be advantageous for them to allocate fewer progeny per host within the cluster. Schmidt & Smith (1985a) studied the mechanism by which *Trichogramma minutum* Riley responded to clustered hosts, and suggested that hosts with more exposed surface areas received more progeny than those with smaller surface areas. Therefore, host eggs that have more neighboring eggs will have a smaller exposed surface area and will receive fewer progeny. Furthermore, eggs that have a higher number of neighboring eggs have more edge-turns performed on them than eggs with fewer or no neighboring eggs (Schmidt & Smith 1985a). Thus, in clustered hosts, edge

turns work as the mechanism of surface area measurements, which subsequently affect the number of progeny allocated (Schmidt & Smith 1985a).

The oviposition model established by the above studies demonstrates the importance of host volume and surface area in *Trichogramma* oviposition behavior. However, most of these studies focused on large, spherical eggs that afford both curvature and large surface areas; even when placed in tightly formed clusters (Schmidt & Smith, 1985a). However, some lepidopterous hosts (*i.e.*, tortricid moths) lay small, flattened eggs which lack curvature (Powell & Common, 1985). For example, the avocado pest *Amorbia cuneana* Walsingham (Lepidoptera: Tortricidae) lays flattened, disk-shaped eggs in irregular egg masses. Additionally, the egg mass is covered by a thin matrix that hardens and extends well beyond the egg mass onto the substrate. Typically, eggs within this mass are stacked upon each other, causing eggs to differ with respect to exposed surface area.

Besides the influence of host physical cues (*i.e.*, size and surface area) on oviposition behavior, previous experience of the female wasp is also important. This experience can be categorized as innate, experience, or learning (Vinson, 1998). Ikawa & Suzuki (1982) demonstrated that if the parasitoid *Apanteles glomeratus* Linnaeus was presented with series of hosts, a larger clutch was oviposited on the first host and subsequent hosts received smaller clutches. One can speculate that successive ovipositions would result in a drop in the female egg complement, resulting in a decrease in the future clutch sizes allocated.

Change in clutch size allocated due to experience will not be observed when large eggs such as *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae) are utilized. These eggs are extremely large and can support a large number of developing *Trichogramma* larvae (Schmidt & Smith, 1985a). Due to their large size, female *Trichogramma* needs to allocate a minimum clutch size to insure the survival of the developing larvae. Hoffman *et al.* (1975) demonstrated that, allocation of a small clutch to a large host would increase larval mortality due to increased risk of bacterial growth. The excess moisture from the host egg is the most probable cause of this bacterial growth. Since it takes only 3 *Manduca sexta* eggs to exhaust *Trichogramma* egg complement (Schmidt & Smith, 1985a), oviposition experience could not have been observed. In order to observe effects of oviposition experience on clutch size allocated one would require to utilizing smaller hosts such as *Amorbia* eggs. These eggs provide a better means of allowing *Trichogramma* to gain oviposition experience because these eggs (individual eggs within a cluster) are smaller and support smaller range of clutch sizes (Honda & Luck, 2001, 2000). Thus, in order to exhaust their egg load complement the wasp needs to parasitize a larger number of individual *Amorbia* eggs.

*Trichogramma platneri* Nagarkatti is an important biological control agent of *A. cuneana* (Honda & Luck, 2000a, 2001; Oatman *et al.* 1983). Personal observations indicate that *T. platneri* females do not utilize the typical examination walk over individual eggs as described in previous work, but walks over the entire egg surface and appears to randomly oviposit within the egg cluster. The objectives of this study were three fold: characterize *T. platneri* oviposition behavior on flattened, irregular *A. cuneana*

egg masses, determine if there is any relationship between host size and the number of progeny allocated, and determine if clutch size adjustment is based on oviposition experience.



## **MATERIALS AND METHODS**

### **Host Cultures**

The larvae of *Amorbia cuneana* were reared based on the modified protocol and artificial diet developed by Johnson & Federici (1982). Adult *A. cuneana* were placed in cylindrical rearing chambers (height: 12 cm, diameter: 12 cm) lined with wax paper, covered on both ends with glass petri dish (diameter: 14 cm). After two days female moths laid their eggs on the wax paper covering the walls of the chambers. The wax paper containing the egg masses was removed from each chamber and by using a scalpel a circular cut was made around each egg mass. To avoid damaging the egg mass, the cut was about 1 cm away from the egg margins. Some of the masses were used to maintain the culture and others were used for experiments. Only 1-2 day old *Amorbia* eggs were utilized in the experiment since *Trichogramma platneri* show higher preference for this age group (Honda & Luck 2000). The parasitic wasp *T. platneri* were obtained weekly from a commercial insectary (Rincon-Vitova Insectaries, Ventura, CA) on parasitized *Sitotroga cerealella* (Oliver) (Lepidoptera: Gelechiidae) eggs affixed to a card. Upon receipt, the cards were placed in capped plastic vials (9 by 5 cm) at room temperature. Female wasps used for the experiment were 24-h old, inexperienced, mated, and fed honey post emergence.

### **Parasitization of the First Six Hosts**

A single wasp was placed in a circular arena (diameter; 2.75 cm) containing a 1-2 day-old *A. cuneana* egg mass. The oviposition behavior of the wasp was continuously observed until a total of 6 eggs within the cluster were parasitized. Under this condition

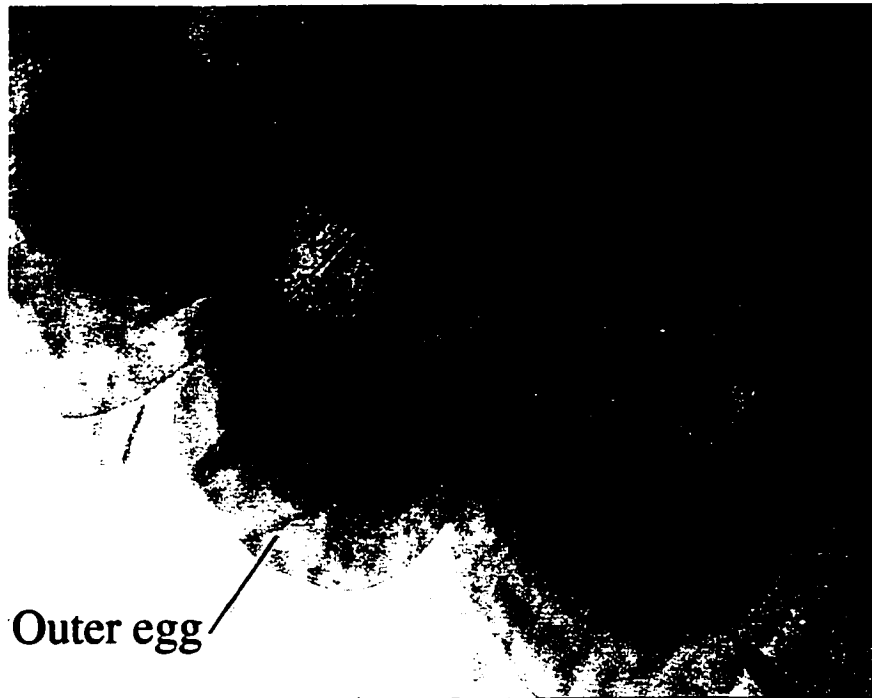
the wasp probably was not able to fully assess the host density. For each egg parasitized the location of parasitization, host size, and number of edge-turns were recorded. The site of each oviposition was marked using food coloring (Schilling<sup>®</sup>), which did not appear to affect the wasp's subsequent oviposition bouts. After oviposition observations were completed, the egg mass was held for 4-5 days until the parasitized eggs turned black. The exposed surface area of each parasitized egg was measured using a dissecting scope fitted with an ocular containing a square grid that was calibrated using a micrometer. The surface area was estimated by counting the number of squares covering an individual egg. These eggs were dissected and their complement of allocated progeny was recorded.

A log-linear analysis test (Bishop *et al.*, 1975; Read & Cressie, 1988) was used in determining the relationship between location of oviposition, number of progeny allocated, number of edge turns, and size of the host. For this analysis the hosts were divided into three size classes (levels): 0.1-0.33 mm<sup>2</sup> (small), 0.34-0.66 mm<sup>2</sup> (medium), and 0.67-1.2 mm<sup>2</sup> (large). The number of progeny allocated and location of oviposition were divided into 3 levels (1, 2, and 3) and 2 levels (inner and outer), respectively. The number of edge turns were divided into three groups (levels): 0-4, 5-10, and more than 10 turns. Finally, the order of oviposition was divided into 6 levels (1<sup>st</sup>, 2<sup>nd</sup> oviposition, etc.) Due to the size of our sample (n=120) the factors mentioned above could not have been pooled together, thus the log-linear test was performed separately on 4 different groups of factors.

The first test-group consisted of progeny allocated, host size, and location of oviposition. The second test-group was progeny allocated, order of parasitization, and location of oviposition. The third group consisted of number of edge-turns performed and the number of progeny allocated. The final group analyzed was the edge-turns and host size. Pearson's correlation analysis was used to test the relationship between the small and large host size classes.

### **Twenty-four Hour Parasitization**

One or two-day old *A. cuneana* egg mass was placed in a circular arena along with 3 one-day old wasps. The first wasp that initiated oviposition behavior was left on the egg mass and the other two wasps were quickly removed. The egg mass was then placed in a test tube for 24-h (12D:12L, 27°C), after which the wasp was removed. This time period (24-h) is considered sufficient time for the wasp to gain oviposition experience, by fully exploring and assessing host density and also allowing the wasp to deposit most of its egg complement. After 4-5 days at room temperature, parasitized eggs turned black. The surface area was measured using the procedure described in the previous section. Individual eggs within the cluster were dissected and the number of progeny allocated to each egg was recorded. The above process was replicated for 15 egg masses. Additionally, to investigate the possible effect of location on oviposition, individual eggs within the cluster of 10 replicates were divided into two classes based on their relative location within a given egg mass. Those eggs completely surrounded by neighboring eggs were designated as "inner", and the eggs in contact with the substrate were designated as "outer" eggs (Fig.1).



**Fig. 1:** Partial image of *Amorbia* egg mass demonstrating the inner and the outer eggs.

Pearson's correlation analysis (Zar, 1999) was used to test the relationship between host size and number of progeny allocated per host in 24-h of parasitization. A two-tailed t-test (Zar, 1999) was also used to analyze the relationship between the number of eggs parasitized in a specific region (i.e. outer vs. inner) and total hosts available in that location. The relationship between average progeny allocated and mean host size in two different locations was analyzed using a two-tailed t-test. Chi-square (Zar, 1999) was used to determine if the frequencies of progeny (i.e., 1, 2, &3) were randomly allocated.

Finally, to test for change in clutch size adjustment between the 24-h parasitization and the first 6 eggs parasitized in the previous experiment, an additional

log-linear analysis was performed on the different clutch sizes allocated between the two groups mentioned above.

## RESULTS

### Host Examination Behavior

In general, three phases characterize the oviposition behavior of *T. platneri* on the *A. cuneana* egg mass: a general examination of egg mass, drumming and turning on individual eggs within the cluster, and oviposition. In the first phase the wasp appeared to randomly examine the egg-mass while drumming it with the antennae without concentrating on any individual egg host within the egg mass. This examination sometimes brought the wasp in contact with the substrate at which time it either turned around and continued the examination or dismounted the egg mass only to return to it after a short time interval. The general examination phase ended when the wasp stopped for a brief moment, which was usually accompanied with grooming. The second phase was limited to individual eggs within the egg mass and was initiated after the brief pause mentioned in the first phase. During this phase of examination, *Trichogramma* walked forward on a single egg while drumming it with its antennae. When either the substrate or neighboring egg margin was contacted, the wasp stopped the forward motion and walked backward while still drumming the host. Quickly after the backward motion the wasp resumed the forward drumming movement and this continued until the host was either accepted or rejected. The average number of turns (edge turns) on hosts was  $2.94 \pm 0.25$  S.E. ( $n = 120$ ). These turns were not uniformly distributed over the host and in the majority of cases were restricted to the small margin of the host and did not encompass all the host's margins. On 20 occasions the host was parasitized immediately upon contact without any examination (edge turns). Overall, no relationship was detected

between the number of edge turns and host size ( $p=0.215$ ) or progeny allocated ( $p=0.703$ ).

The third phase began with the acceptance of the host and display of stereotypical oviposition behavior, which was characterized by the lowering of the abdomen and insertion of the ovipositor into the host (Suzuki *et al.*, 1984). On few occasions ( $n=3$ ) the oviposition posture was assumed on the substrate away from the host and was abandoned only when the wasp failed to penetrate the substrate with the ovipositor. The rejection of the host occurred at any of the three stages.

### **Parasitization of the First Six Hosts**

*Trichogramma platneri* took approximately 3-h to parasitize 6 eggs within a given host cluster ( $n = 20$ ) and on average each host received  $1.78 \pm 0.04$  ( $n = 120$ ) progeny. Twenty three percent of the eggs ( $n=28$ ) received one individual while 75% ( $n=90$ ) and 2% ( $n=2$ ) were allocated two and three progeny, respectively, which were statistically different from each other ( $\chi^2 = 19.4$ ,  $df = 2$ ,  $p<0.05$ ). Wasps more often selected the outer than the inner eggs, but this was only significant in the first ( $\chi^2 = 7.2$ ,  $df = 1$ ,  $P<0.05$ ) and third ( $\chi^2 = 5.2$ ,  $df = 1$ ,  $P<0.05$ ) bouts of oviposition.

Inner hosts averaged  $0.4152 \pm 0.05 \text{ mm}^2$  ( $n = 49$ ) in size with mean progeny of  $1.75 \pm 0.06$ , while the outer hosts averaged  $0.5677 \pm 0.03 \text{ mm}^2$  ( $n = 71$ ) in size with  $1.79 \pm 0.045$  progeny. Statistically there was no relationship between the size of the host and the progeny allocated in the specified regions (t-test,  $p>0.05$ ).

The results of Log-linear analysis for the number of progeny allocated, egg size, and location of oviposition, revealed a possible working model of [Egg size\*Location]

(Table 1). A higher percentage of outer eggs were 0.34 mm<sup>2</sup> and larger (55%) as opposed to 36% of inner eggs. However, no relationship was detected between host size and number of progeny allocated ( $p=0.397$ ). Analysis on location of oviposition, progeny allocation, and order of oviposition, generated no working model (Table 1). Log-linear analysis between egg size and edge-turns also showed no significant relationship between the two ( $p=0.215$ ), furthermore no relationship was detected between edge-turns and progeny allocated ( $p=0.703$ ). Finally, there was no relationship detected between the number of progeny allocated and the smallest and largest egg classes (Pearson's Correlation Index,  $R=0.297$ ).

**Table 1: Log-linear analysis of, progeny allocated, location of oviposition, order of oviposition, Edge turns, and Egg size in generating the best-fit model. Log-likelihood ratios (LR) are presented for the best-fitting log-linear models.**

Terms	Best-fit model	LR	P
Prog., Egg size, Loc.	Egg size*Loc.	16.6	0.002
Prog., Order, Loc.	No Relationship	--	>0.05
Edge turns, Egg size	No Relationship	--	>0.05
Edge turns, Prog.	No Relationship	--	>0.05
Progeny allocated (Prog.), location of oviposition (Loc.), order of oviposition (Order)			



## 24-h Parasitization

*Amorbia cuneana* egg masses consisted of  $30.3 \pm 1.0$  eggs, with  $14.6 \pm 0.96$  and  $15.7 \pm 1.14$  categorized as outer and inner eggs, respectively. The size of the individual eggs ranged from 0.1 to 1.3 mm<sup>2</sup>. *Trichogramma platneri* parasitized  $23.3 \pm 1.83$  eggs within each cluster in 24-h, and allocated  $1.53 \pm 0.04$  (n=342) progeny per host. Fifty four percent of the eggs received one individual (n = 185), while 39% (n = 136) and 6% (n = 20) were allocated two and three individuals respectively, which were statistically different from each other ( $\chi^2 = 90$ , df = 3,  $P < 0.05$ ). Only one host egg received five progeny.

The number of eggs parasitized in the inner and outer zones relative to the total number of hosts available in the respective areas was not statistically significant (t-test,  $p=0.925$ ). Furthermore, larger hosts did not receive more progeny than smaller hosts; 14 out of the 15 replicates showed no correlation between the size of the host and number of progeny allocated in 24-h parasitization (Table 2). The presence of an outlier in one of the samples (egg mass 3), due to a very large host (1.3 mm<sup>2</sup>), caused it to show a significant relationship between the host size and progeny allocated. This point was almost 3 standard deviations away from the mean, thus it was removed (Zar, 1999). After removal the sample showed no significant relationship host surface area and number of progeny allocated.

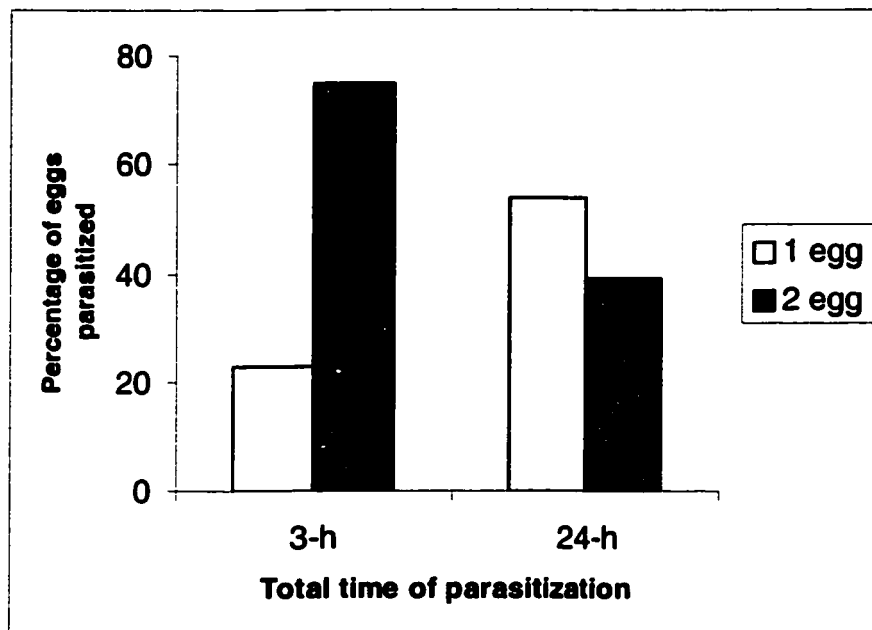
**Table 2: The relationship between progeny allocated and the host size in a 24-hr period using Pearson's Correlation Analysis ( $\alpha = 0.05$ ). The sample with the asterisk\* showed a significant relationship but this was due to an outlier point. Its subsequent removal showed that there is no relationship<sup>a</sup>.**

<b>Egg mass</b>	<b>Calculated R-value</b>	<b>Critical R-value</b>	<b>Egg mass</b>	<b>Calculated R-value</b>	<b>Critical R-value</b>
1	0.074	0.396	9	0.390	0.514
2	0.206	0.482	10	0.435	0.482
3	0.574*	0.482	11	0.113	0.456
4	0.033	0.444	12	0.192	0.361
5	0.169	0.444	13	0.064	0.396
6	0.378	0.396	14	0.060	0.396
7	0.301	0.396	15	0.251	0.361
8	0	0.444			

<sup>a</sup> The outlier point was more than 2 S.D. away from the mean, therefore, removing the point was acceptable.

### **Comparing Oviposition Rates Between 24-h and First Six Hosts Parasitized**

Log-linear analyses between clutch sizes allocated at different times were significantly different from each other ( $\chi^2 = 41$ ,  $df = 1$ ,  $P < 0.001$ ). In first six eggs parasitization a higher percentage of eggs received 2 progeny (76.3%) than 24-h parasitization (42.4%). More eggs were allocated 1 progeny in 24-h (57.6%) than 3-h (23.7%) parasitization (Fig. 2).



**Fig. 2:** The percentage of 1 and 2 progeny allocated by *T. platneri* between the first six eggs parasitized (3-h) and 24-h oviposition bouts.

## DISCUSSION

The oviposition behavior for *T. platneri* is different from the behavior described by Schmidt & Smith (1989, 1987a, 1985a). No relationship was detected between the exposed surface area of a host and clutch size allocated to it. Furthermore, the number of edge-turns performed on a given host was independent of surface area and the number of progeny allocated to it.

The host examination of *T. platneri* on *A. cuneana* is different than the behavior recorded by Schmidt & Smith (1987a, 1985a) for *T. minutum* on *Manduca sexta*. This oviposition behavior is more akin to parasitization behavior described by Luck *et al.* (1982) for *Aphytis* (Hymenoptera: Aphelinidae) parasitizing armored scales. When female *Trichogramma* contacted individual egg margins within *Amorbia* egg mass, it simply walked backward and shifted the examination in another direction instead of turning around and continuing the examination in another direction as predicted by Schmidt & Smith (1989, 1987a, 1987b). This backward motion after contacting egg margins is similar to the examination behavior of *Aphytis* (Luck *et al.*, 1982). This might be attributed to the physical similarities between the features of individual *Amorbia* eggs and armored scale coverings. Both the *Amorbia* eggs and scale coverings are flat, disk-shaped and lack curvature thus the turning behavior reported by other researchers (Schmidt & Smith, 1989, 1987a, 1987b) is not required and a simple backward motion suffices.

There are two possible explanations for detecting no relationship between the clutch size allocated and host size (surface area). One possible explanation is that wasps

cannot recognize where the margins of individual hosts within the egg mass and perceive it as one large host. Thus, the progeny are allocated randomly to different parts of the host. Another possible explanation is that size differences are too small for the wasps to recognize. The difference between the largest egg-class may not be significantly different from the intermediate or smaller egg classes to warrant changes in clutch size (J.J.B. Smith, University of Toronto, personal communication).

The first point addressed above can be easily refuted. When observing *T. platneri* it is obvious that the wasps are restricting their examination to individual host eggs within the cluster. Whenever wasps contacted the host margins (substrate or other hosts) they walked backward and shifted their walk either to the left or the right and resumed examination. Therefore, they are able to recognize boundaries of individual eggs in a cluster. The second point is possible, but studies have suggested that female wasps can discriminate between small differences in host sizes and subsequently allocate different clutch sizes (Klomp & Teerink, 1962). In their study, *Ephestia kuhniella* Zeller (Lepidoptera: Pyralidae) with a diameter of 0.3 mm on average supported 1.1 progeny per host, while *Bupalus piniarius* Linnaeus (Lepidoptera: Geometridae) supported a larger clutch (6.7 progeny/host) even though its diameter was only 0.6 mm larger than *E. kuhniella* (Klomp & Teerink, 1962). This clearly demonstrates that *Trichogramma* can detect small changes in host size and appropriately adjust clutch size. Thus small differences in host size do not necessarily mean that the wasps will not adjust clutch size. It must be noted that despite the possible ability to detect small changes in size, the wasps in this study did not change their clutch size based on these differences. No relationship

was detected between the host size and clutch size even when the smallest and largest egg size-classes were compared with each other.

Nonetheless, there appears to be a fitness component associated with different clutch sizes allocated by *T. platneri* to *Amorbia* eggs. Honda & Luck (2001) have shown that the fecundity of *T. platneri* offspring decreased as the number of emerging progeny per host increased. If one progeny is allocated to an *Amorbia* egg, the emerging adult will have a 24-h fecundity that is almost two times greater than adults emerging from hosts that had two progeny allocated to them. This fecundity was even smaller for emerging wasps from host that had three progeny allocated to them (Honda & Luck, 2001). Therefore, there is a significant biological difference between emerging wasps at 1, 2, and 3 progeny per host. This difference in fecundity is directly related to the number of conspecifics that emerge from a single host (Bai *et al.*, 1992; Honda & Luck, 2001). As more progeny are located to a host, the average size of emerging wasps is diminished (Klomp & Teerink, 1962, 1967; Suzuki *et al.*, 1984; Waage & Ng, 1984) which has a negative effect on the wasp's fitness (Hohmann *et al.*, 1988; Kazmer & Luck, 1995). Furthermore, the percentage of surviving larvae will decrease because of intraspecific competition (Klomp & Teerink, 1967; Suzuki *et al.*, 1984). Therefore, a trade-off exists between the number of eggs allocated to a host and the number and size of emerging wasps. The trade-off in this study was in the size of the emerging progeny, which was demonstrated to be related to fecundity of these wasps (Honda & Luck, 2001).

No relationship was detected between host size and number of progeny allocated, which stands in contrast to other studies (Klomp & Teerink, 1962, 1967;

Waage & Ng, 1984; Schmidt & Smith, 1985b, 1987b). Nevertheless, the data indicates that wasps are adjusting their clutch size over time, subsequently changing the fitness of emerging progeny. In the first experiment, within the first 6 eggs parasitized the majority of the hosts received 2 progeny (75%) while in the 24-h parasitization a smaller proportion were allocated the same complement of progeny (39%). It seems that, as more hosts are parasitized the wasps at some point begin to lay 1 versus 2 eggs per host.

There are a few possible mechanisms governing the clutch size adjustment over time by *T. platneri* when encountering *Amorbia* egg mass: experience, egg load, and frequency of host encounter. Rosenheim & Rosen (1991) demonstrated that egg load and experience do influence clutch size adjustment in some parasitoids. In their study, parasitoids with fewer eggs and recent oviposition experience deposited smaller clutches than the ones with larger egg load. Since in 24-h parasitization the wasps encountered a higher number of individual hosts, their oviposition experience was higher than the group parasitizing the first 6 eggs. This could explain why the wasp with less oviposition experience allocated larger clutch sizes than the wasps in the 24-h parasitization group. Furthermore, adjustment of progeny allocated appears to be regulated by some measure of host finding. Schmidt & Smith (1987c) demonstrated that hosts which are separated by 2-5 mm were allocated different clutch sizes. Hosts that were separated by 2 mm had a significantly smaller clutch sizes allocated to them than hosts separated by 3-5 mm (Schmidt & Smith 1987c). They speculated that the distance traveled by the wasps or the time interval between ovipositions might play a role in clutch size adjustment. *Amorbia* eggs used in this study are highly clustered and the distances between individual eggs

within the egg mass is nonexistent, thus the frequency of host encounter by *Trichogramma* is high, which may have caused the reduction seen in clutch sizes allocated over time. Ultimately, it appears that the wasps maximize their fitness by adjusting their progeny allocation over time so that most hosts contain a single host.

Oviposition behavior of *Trichogramma platneri* on *A. cuneana* is clearly different than the established model for parasitoids of this genus. The mechanism for oviposition behavior on egg masses appears to be imprecise. In this study, *Trichogramma* females were seen to parasitize hosts without examining them and in few occasions the wasps were observed assuming oviposition posture even though they were away from the host. This can be attributed to the presence of chemical cues either from the matrix covering the egg mass or cues left by female moth (*i.e.* scales, etc.) which have been shown to play a major role in host selection (Lewis *et al.*, 1972; Miura & Kobayashi, 1997; Vinson, 1976). For example, Miura & Kobayashi (1997) were able to induce oviposition behavior by *T. chilonis* Ishii on Sealon film that was treated with moth scale secretions. These observations coupled with the fact that *Trichogramma* females have been observed attempting to oviposit in inanimate objects such as globules of Mercury and glass fragments (Salt, 1935). Thus one cannot characterize the oviposition behavior of these wasps to single model and should recognize the plasticity of oviposition of these insects.



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